Increasing plant group productivity through latent genetic variation for cooperation

Samuel E. Wuest[1,2,3*], Nuno D. Pires[1], Shan Luo[4], Francois Vasseur[5], Julie Messier[6], Ueli Grossniklaus[1], and Pascal A. Niklaus[2]

1) Department of Plant and Microbial Biology & Zurich-Basel Plant Science Center, University of Zurich, Zollikerstrasse 107, CH-8008 Zurich, Switzerland

2) Department of Evolutionary Biology and Environmental Studies & Zurich-Basel Plant Science Center, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

3) Group Breeding Research, Division Plant Breeding, Agroscope, Müller-Thurgau-Strasse 8, CH-8820 Wädenswil, Switzerland

4) Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, United Kingdom

5) CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France

6) Department of Biology, University of Waterloo, 200 University Avenue West, Waterloo N2L 3G1, Canada

*correspondence to: Samuel E Wuest (samuel.wuest@agroscope.admin.ch)

Abstract

Historic yield advances in the major crops have to a large part been achieved by selection for improved productivity of groups of plant individuals such as high-density stands. Research suggests that such improved group productivity depends on "cooperative" traits (e.g. erect leaves, short stems) that – while beneficial to the group – decrease individual fitness under competition. This poses a problem for some traditional breeding approaches, especially when selection occurs at the level of individuals, because "selfish" traits will be selected for and reduce yields in high-density monocultures. One approach therefore has been to select individuals based on ideotypes with traits expected to promote group productivity. However, this approach is limited to architectural and physiological traits whose effects on growth and competition are relatively easy to anticipate.

Here, we developed a general and simple method for the discovery of alleles promoting cooperation in plant stands. Our method is based on the game-theoretical premise that alleles increasing cooperation incur a cost to the individual but benefit the monoculture group. Testing the approach using the model plant *Arabidopsis thaliana*, we found a major effect locus where the rarer allele was associated with increased cooperation and productivity in high-density stands. The allele likely affects a pleiotropic gene, since we find that it is also associated with reduced root competition but higher resistance against disease. Thus, even though cooperation is considered evolutionarily unstable, conflicting selective forces acting on a pleiotropic gene might maintain latent genetic variation for it in nature. Such variation, once identified in a crop, could be rapidly leveraged in modern breeding programs and provide efficient routes to increase yields.

Keywords: plant competition and cooperation; tragedy of the commons, GWAS; pleiotropy; Darwinian agriculture; evolutionary agroecology

Introduction

Crop breeding is currently undergoing fundamental transformations. Speed breeding and genomic prediction can shorten generation times and increase effective population sizes, leveraging rates of phenotypic change to unprecedented levels [1,2]. At the same time, large-scale, high-throughput phenotyping platforms have become available and allow for the simultaneous quantification of multiple traits in ever larger greenhouse and field settings [3]. Yet some studies suggest that current rates of yield increase are insufficient to meet growing demands from increasing human and animal population under a changing climate [4,5].

Historically, the highest rates of yield increase were achieved in the middle of the 20th century, at the beginning of the "Green Revolution". Combining breeding with improved management, yield potentials of major crops such as wheat and tropical rice approximately doubled in only a few plant generations [6–8]. In retrospect, these gains in yield potential have been unusually large. In contrast to most classical breeding that operates through selection on polygenic variation, they were largely realized by capitalizing on single genes, notably by the introgression of discrete but pleiotropic dwarfing alleles with major effects on plant form and function [9,10]. These alleles resulted in smaller and less bushy individuals, which diverted less resources to competition and allocated more into reproduction, i.e. into grain yield. The resulting more "cooperative" genotypes could be cultivated in high-density stands, which resulted in an increased crop yield per unit land area, with little productivity increase at the individual level. In other words, a trade-off between individual fitness and group-level yield was exploited to promote yield in well-fertilized high-density stands [8,11–16]. This trade-off, however, also causes the traits that benefit the group to be selected against in mixed or segregating populations containing larger, more competitive individuals, where cooperative individuals have lower relative fitness [14,17].

A key lesson from the "Green Revolution" thus is that selection for competitive individuals must be avoided to achieve the highest-possible yields. One way to achieve this in breeding is to anticipate "ideotypes" with a suite of phenotypic traits that reduce competition and thereby promote cooperation. Desirable traits are, for

example, a short stature, erect leaves, and a compact root system [12,13,18]. However, a limitation of ideotype breeding is that the specific trait variation relevant for high crop yield in high-density groups often remains elusive to the human observer, especially for below-ground traits. In principle, this can be avoided by shifting the focus on selection for quantitative genetic variation for cooperative traits at the group level [19–21], but this is often impractical (especially early in the breeding cycle), requiring more land and resources for phenotyping. Further, when genetic variation for the trait of interest does not exists in the breeding population, it first must be discovered in a wider crop population or in wild relatives (e.g. secondary gene pool).

Plant cooperation among unrelated individuals rarely evolves in natural systems because plants often grow in communities of unrelated individuals, a setting under which cooperative phenotypes have low fitness [22]. However, if latent genetic variation for cooperation exists in nature, it could potentially be leveraged in breeding [23]. The difficulty, however, is to discover relevant alleles in a diverse set of plants, in particular when they do not correspond to classical ideotypes. Here, we present a methodological framework for the discovery of such alleles. We aimed for such a framework to be as general and unbiased as possible, in order to detect yield or biomass gains (or any other performance measure) that emerge from any type of cooperation, including for unknown resources and through unidentified traits. Specifically, we designed competition experiments and corresponding analytical tools that allow to rank plant genotypes on a scale ranging from “competitive” to “cooperative”. We then applied these methods in a proof-of-concept experiment with a population of *Arabidopsis thaliana* genotypes and produced a genetic map of a group vs. individual (G-I) performance trade-off. Variation at one genomic region was strongly associated with variation along this trade-off, whereby the allele of minor frequency promoted cooperation. However, the identified genetic variants were neither associated with individual- or monoculture-level productivity alone. They only became evident when mapping the G-I performance trade-off itself. We then showed in separate experiments that the associated genetic polymorphisms allowed predicting productivity responses of genotypes along plant—density gradients. We argue that the method we present here has a large application potential,

not least because of recent advances in technology including genome-wide association studies (GWAS) and large-scale phenotyping that make these methods widely applicable.

Results

Quantifying a plant group-vs-individual (G-I) performance trade-off by growing genotypes in different social contexts

The core principle of our method is to measure the performance of a set of genotypes in different "social contexts" [24], allowing for the quantification and subsequent genetic mapping of variation in a G-I trade-off. To achieve this, we grew individuals of a set of genotypes (1) in monoculture, i.e. we confronted them with their own social strategy, and (2) in competition with a set of "tester" genotypes that represent the range of social strategies present in the population. According to game theory, the most cooperative genotype of the set will perform best with similarly cooperative neighbors (i.e. as a group in monoculture) but will lose when facing selfish, highly-competitive neighbors (i.e. as an individual in mixtures). Conversely, the most competitive genotype will perform worst when grown with similarly competitive neighbors but will win when facing a cooperative neighbor. Comparing the performance of a genotype in monoculture group relative to the performance with the tester set therefore allows to quantify the genotypes' G-I performance trade-off (**Fig. 1**) and thereby rank all genotypes on a continuum between cooperative and competitive. In principle, this approach is applicable to any species, but for simplicity we tested it with an association panel of 98 natural *A. thaliana* accessions – a subset of the RegMap population [25]. Aboveground dry matter production (shoot biomass) served as the measure of performance (Materials and Methods), but any other target characteristic such as agricultural yield could also be used. Each of the 98 focal genotypes was grown in a pot that contained two congenotypic individuals (genotype monoculture), and additionally as individual in ten further pots with one individual from each of ten tester genotypes (genotype mixtures; **Fig. 1A,B**; Supplementary **Fig**. **S1**). The design was replicated in two blocks.

148 As expected, competitive interactions among individuals were strong, with large
149 negative effects of average tester shoot biomass (average across all pots) on shoot
150 biomass of the focal genotypes (ANOVA $F_{1,960} = 88.23$; $P < 0.001$). To evaluate the
151 group vs. individual (G-I) performance trade-off of genotypes, we related the mean
152 shoot biomass of the target genotypes in monocultures to their average individual
153 biomass when grown in competition with tester genotypes (individual performance
154 in mixed stand; **Fig. 1C**). Not surprisingly, across genotypes, group and individual
155 performance were highly positively associated, with more vigorous genotypes
156 producing more biomass both in monoculture groups and as individuals subject to
157 competition by testers. This relationship was also non-linear (second degree
158 polynomial; $F_{1,95}$=8.4, P=0.005 for quadratic term), possibly because space became
159 progressively limited as plant size increased [24,26]. However, the exact nature of
160 this deviation from linearity is unimportant since we treated the overall relationship
161 as heuristic. We then used the distance of each genotype's data from this empirical
162 relationship to locate each genotype on an orthogonal axis that quantified the G-I
163 trade-off (Methods and **Fig. 1C**). In other words, this procedure transforms the
164 separate values for group performance in monoculture and mean individual
165 performance in mixtures into two orthogonal metrics: the position along the overall
166 relationship reflects general genotypic vigor (e.g. increased productivity due to better
167 adaptation to the specific growth conditions), and the position perpendicular to the
168 general relationship reflects a G-I trade-off value that characterizes the communal
169 properties of the focal genotype (inset **Fig. 1C**). Specifically, the G-I value is
170 positive for more cooperative genotypes, which have relatively lower individual
171 performances in mixtures (competitive environment) but a higher performance in
172 monoculture (cooperative environment).

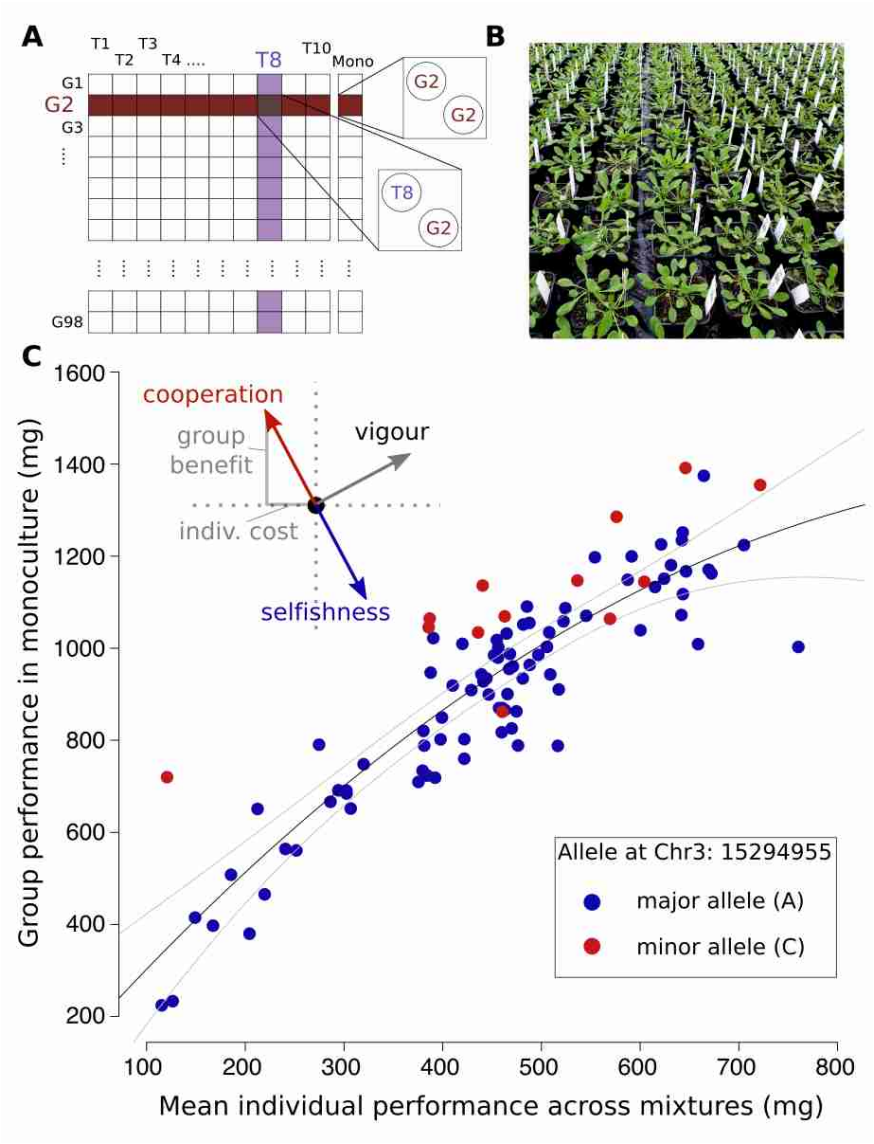


Figure 1: A general method for the genetic dissection of the group-vs-individual performance (G-I) trade-off. (A) Experimental design of the competition experiment. G1, G2, … G98: focal genotypes sampled from the RegMap panel of natural *A. thaliana* accessions. T1, T2, … T10: tester genotypes representing a range in plant size to reflect a large portion of the genetic variation present within *A. thaliana*. **(B)** Experimental setup. **(C)** Relationship between a genotype's mean performance (shoot biomass) as an individual across all mixtures with tester genotypes and its group performance in monoculture. Black line: second degree polynomial with 99% confidence intervals. The inset outlines three of many possible genetic effects a hypothetical allele could have on a genotype's strategy: variation along the mixture-vs-monoculture regression describes variation in vigor, and variation perpendicular to the regression describes the G-I performance trade-off. Red and

184 blue dots show genotypes carrying different alleles at position 15'294'955 on chromosome 3
185 (see below), whereby red alleles confer a more cooperative strategy.
186
187 **Genome-wide association mapping identifies allelic variation associated with**
188 **G-I tradeoff**
189 Next, we performed genome-wide association tests for the genotypic G-I trade-off
190 value. Genome-wide polymorphism data of our population were available through
191 the RegMap panel and single nucleotide polymorphism (SNP) information was
192 available for 214,000 sites. The G-I trade-off value was significantly associated with
193 a major effect locus on chromosome three (**Fig. 2A,B**). The rarer allele (C-allele)
194 was found in 18% of the RegMap population and was associated with lower
195 individual but higher group performance, i.e. with increased cooperation (**Fig. 1C**).
196 The SNP with the strongest association resides in the center of a transposon-rich
197 region and explained approximately 25% of the variation in the genotypic G-I trade-
198 off values (**Fig. 2C**). Direct mapping of untransformed data, i.e. of variation in either
199 individual or monoculture group biomass alone, did not reveal any significant
200 associations (Supplementary **Fig. S2A,B**). This was expected, because such an
201 analysis fails to separate general vigor from the G-I trade-off value that we used here
202 to quantify cooperative properties. A more detailed genomic analysis based on a
203 subset of 68 genotypes for which genome-wide re-sequencing data are available
204 [27] revealed association signals across many polymorphisms in a region of
205 approximately 150 kb around the identified RegMap SNP, all in high linkage
206 disequilibrium (**Fig. 2B**).

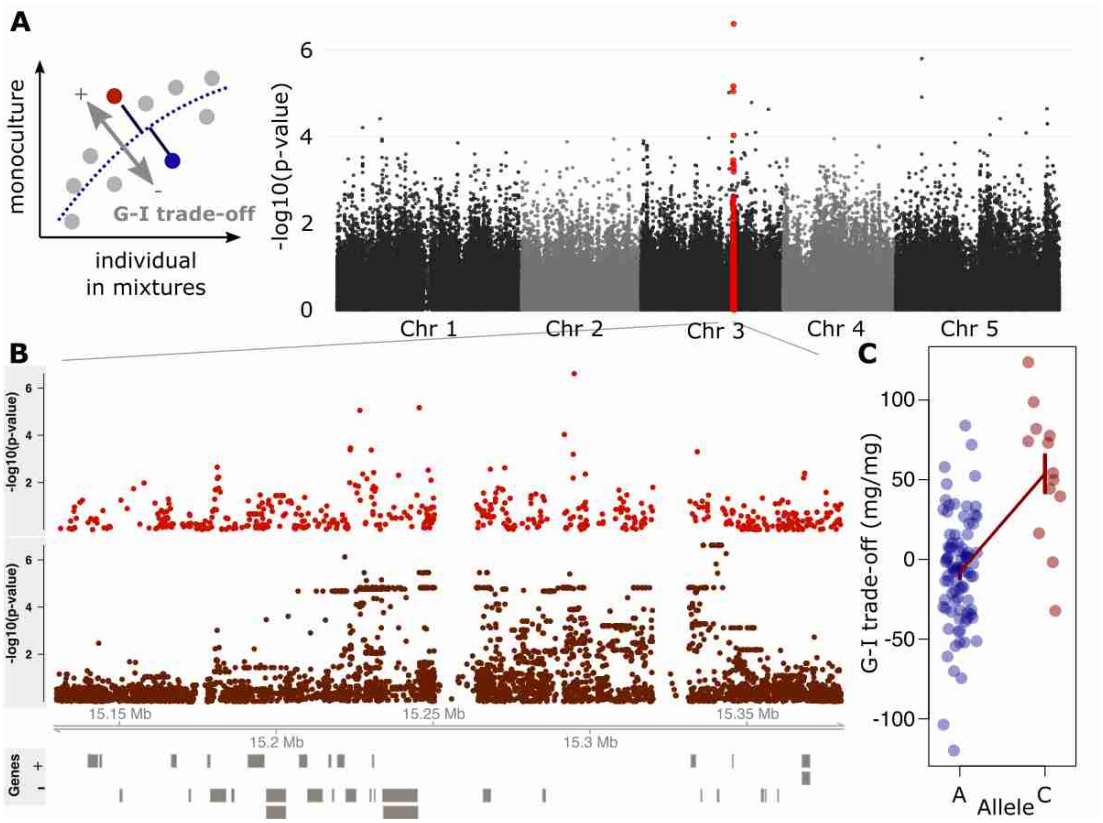
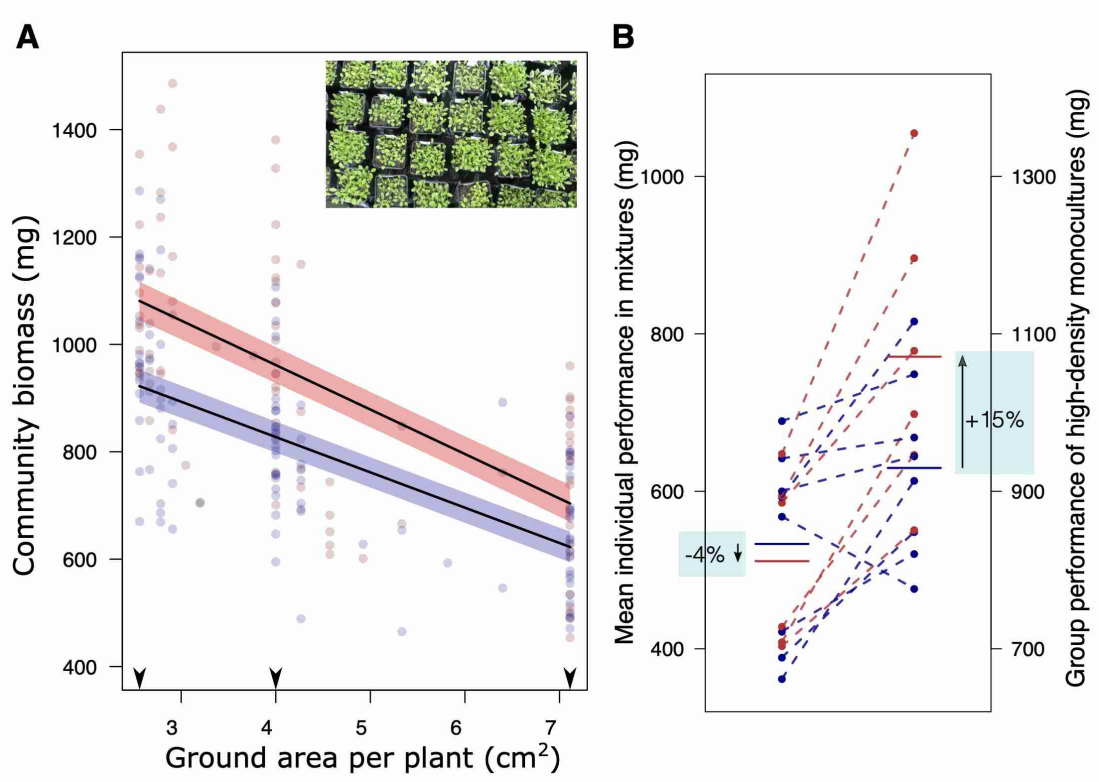


Figure 2: Allelic variation at a major effect locus affects the group-vs-individual performance (G-I) trade-off in *A. thaliana*. (A) Manhattan plots of genome-wide association tests for variation in the G-I trade-off, based on the 250k SNP chip data. The genotypic G-I trade-off value is the distance from the overall trend between group and individual performance in monoculture and mixtures, respectively (inset). **(B)** Zoom in on a segment of chromosome 3, showing Manhattan plots of either an association analysis using SNP chip polymorphisms (top), or, for a subset of 68 genotypes, genome-wide re-sequencing polymorphisms (bottom). Models of protein-coding genes are drawn as boxes below, on either + (upper) or – (lower) strand. **(C)** Association of variation at SNP 15'294'955 and the G-I trade-off. Error bars denote means ± s.e.

Cooperative allele improves monoculture productivity at high density

To experimentally validate our finding of enhanced cooperation (i.e. of improved group performance in lines carrying the minor allele at SNP 15'294'955), we performed a stratified sampling of genotypes for plants of different sizes carrying either allele and grew these in stands of increasing planting density. Cooperative plant traits typically improve group performance especially at high planting densities

225 [15,28,29]. Genotypes carrying the cooperation-associated allele at SNP 15'294'955
226 indeed exhibited superior productivity at the highest sowing density (+15% biomass,
227 average across all genotypes; **Fig. 3 A,B**; ANOVA $F_{1,10.6}$=7.5 , P=0.02), despite
228 slightly lower individual performance across mixtures in the competition experiment
229 (- 4% biomass in mixtures, **Fig. 3B**). As anticipated, group performance gains were
230 more pronounced at higher densities relative to those at lower densities (**Fig. 3A**;
231 ANOVA $F_{1,14.9}$ = 7.0, P = 0.019 for allele × ground area per individual). These results
232 demonstrate that the molecular method presented here is able to predict group-level
233 features that cannot be deduced from individual-level properties, and that these allow
234 improving monoculture stand productivity.



236 **Figure 3: Genotypes carrying the allele for cooperation exhibit superior**
237 **monoculture performances at high-density**. **(A)** Changes in monoculture biomass of
238 genotypes carrying either the cooperation-associated allele (C-allele, red) or the alternative
239 allele (A-allele, blue) across a realized planting density gradient. Lines show linear
240 regression estimates ± s.e. Arrowheads show-per plant areas at the sown target densities,
241 which were not always realized due to seedling mortality. **(B)** Comparison of genotype's
242 mean individual shoot biomass in mixtures versus monoculture biomass at densities of 25

243 plants per pot (2.56 cm^2 per plant). Horizontal lines: mean values across all genotypes
244 carrying either allele. Red and blue: cooperation-associated allele (C-allele) and alternative
245 allele (A-allele) at SNP Chr 3 15'294'955, respectively. Note the different scales of the left
246 and the right y-axes.
247

248 **Reduced root allocation is associated with enhanced cooperation**

249 We next explored the relationship between the allele for cooperation and
250 phenotypic traits to identify potential mechanism underlying enhanced cooperation.
251 We measured two traits that characterize growth and resource-acquisition strategies
252 of the genotypes in our panel. Specifically, we measured rosette diameter because
253 rosette lateral size affects light harvesting, and monoculture root-to-shoot ratio as
254 indicator of relative investment into below-ground nutrient aquistion (Methods). We
255 further included two publicly available phenotypic traits into our analysis [30],
256 namely flowering time in the field and vegetative growth rate. Genotypes carrying
257 the allele for cooperation had significantly lower root-to-shoot ratios (ANOVA
258 $F_{1,95}$=5.13, P=0.026; effect size: 19% lower root/shoot ratio), and these were
259 significantly negatively associated with their G-I trade-off value (ANOVA
260 $F_{1,95}$=18.4, P<0.001; **Fig. 4A and B**). None of the other traits examined showed such
261 an association (**Fig. 4 A** and Supplementary **Fig. S3**). We confirmed that this pattern
262 of lower root-to-shoot ratio in cooperative genotypes holds across environments by
263 conducting an independent experiment, where we explored this effect in both
264 monocultures and in isolated individual plants, and in a different soil type (**Fig. 4C**,
265 and Supplementary **Fig. S3**). Overall, our findings indicate that reduced relative root
266 growth is part of a genetically fixed strategy associated with enhanced cooperation.

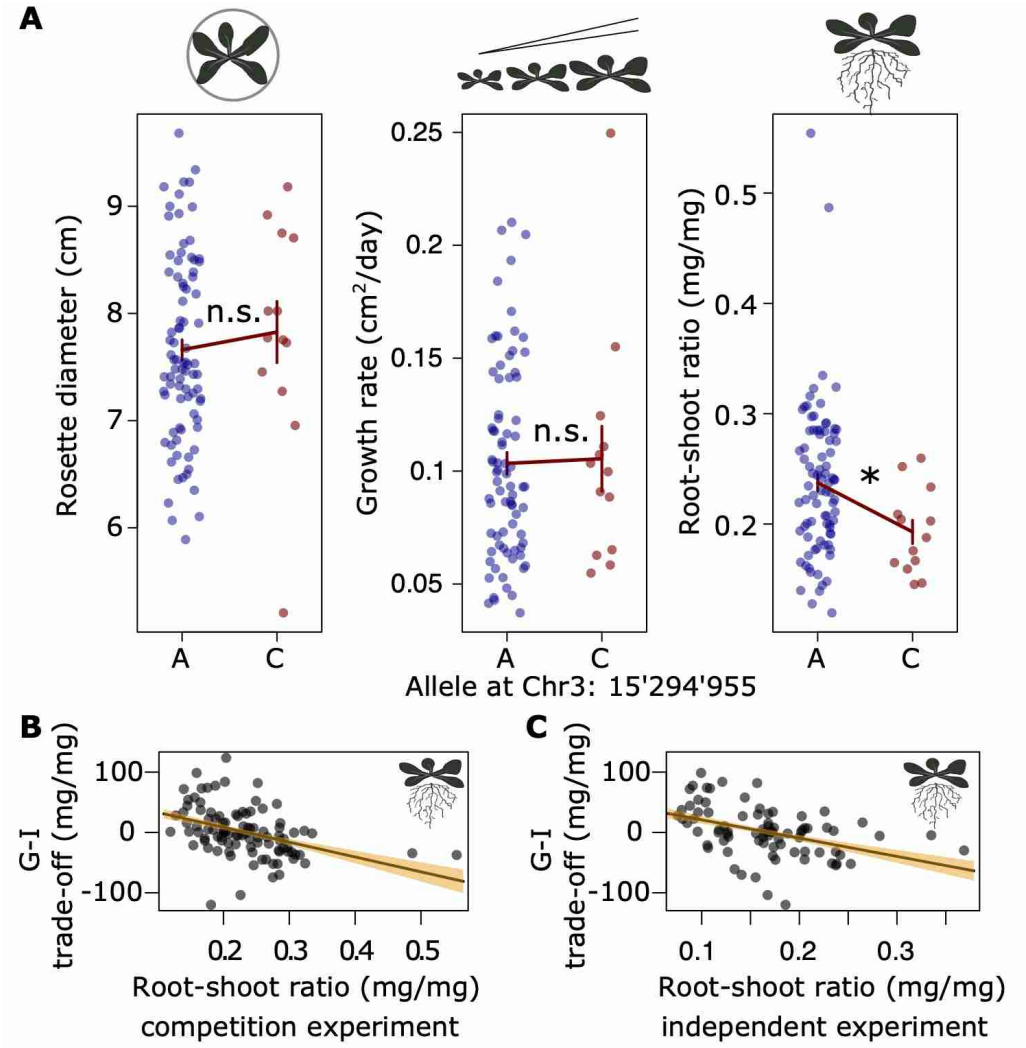
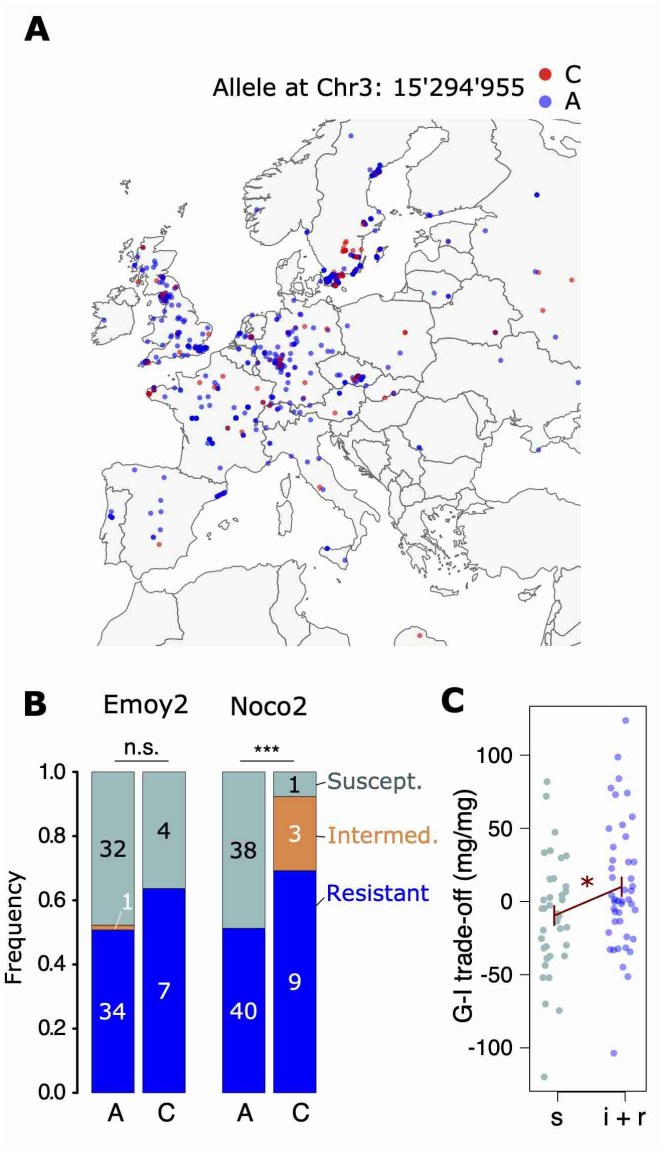


Figure 4: Altered allocation to roots but not growth or life history is associated with increased levels of cooperation. (A) Association of allelic variation at SNP Chr3:15'294'955 with variation in traits related to different plant strategies. **(B)** and **(C)** Relationship between the G-I performance trade-off and plant root-to-shoot ratio in monocultures of the competition experiment shown in Fig 1 (B) or monocultures of an independent experiment (C; see also Methods and Suppl. Fig. S3). Bars and regression lines show means ± s.e.; * ANOVA $P < 0.05$; n.s.: not significant.

The cooperative allele is geographically widespread and associated with pathogen resistance

Evolutionary game theory predicts that an allele which promotes cooperation will be selected against in a natural plant population, except under special circumstances [31]. We were thus surprised that the allele for cooperation that we identified is

280 found over a wide geographic range and at remarkably high frequency (**Fig. 5A**;
281 minor allele frequency 18%). Genes often have multiple functions, and we therefore
282 expected that in natural populations, conflicting selective forces acting on such
283 pleiotropic genes (or on genes in tight linkage) might underpin the persistence of
284 alleles for cooperation [32]. Examining genes in the identified genomic region, we
285 found *AtMIN7*, a documented regulator of both growth and defense. The AtMIN7
286 protein targets pathogen effectors that suppress the plant immune response [33].
287 Importantly, variation at the *AtMIN7* gene is associated with resistance against
288 *Hyalonperonospora arabidopsidis*, an obligate pathogen of *A. thaliana* causing
289 downy mildew [34]. Analyzing this published data on resistance against different
290 strains of *H. arabidopsidis,* (incl. Noco2 and Emoy2*)* we found that the cooperation-
291 associated allele indeed was highly significantly associated with partial or full
292 resistance against strain Noco2 (**Fig. 5B**, Fisher's exact test; $P<0.001$). The resistance
293 level against Noco2 also explained significant amounts of variation in the G-I trade-
294 off value of our genotypes (ANOVA $F_{2,79}=3.57$, $P=0.03$, **Fig. 5C**). We therefore refer
295 to this naturally-occurring genetic variation as *latent* variation for cooperation, since
296 contributions to pathogen resistance rather than cooperation has likely maintained the
297 minor allele in *A. thaliana.*



298 **Figure 5: The cooperation-associated allele exhibits a wide geographic distribution**
299 **and is correlated with increased race-specific pathogen resistance. (A)** Occurrence of
300 natural *A. thaliana* accessions carrying the allele for cooperation (red 'C') or the alternative
301 allele (blue 'A') across sampling sites in Europe. **(B)** Association of Chr 3 SNP 15'294'955
302 with resistance or susceptibility against strains of *Hyalonperonospora arabidopsidis* (Emoy2
303 and Noco2), based on published data [34]. Numbers indicate genotype counts. n.s. = no
304 significant difference **(C)** Association of Noco2 resistance levels with the G-I trade-off. s =
305 susceptible, i+r = intermediately and fully resistant.
306
307

308 **Lines carrying the cooperator allele have a competitive advantage in**
309 **conditions of high disease pressure**

310 Further evidence for the idea that the allele for cooperation is advantageous in
311 environments with pathogens emerged from an additional experiment in which we
312 quantified individual allele's benefits (payoffs) in well-defined competitive
313 interactions. For the experiment, we isolated four different pairs of near-isogenic
314 lines (NILs) from Shahdara×Bayreuth recombinant inbred lines [35], i.e. pairs of
315 nearly identical genotypes in which allelic variation was restricted to the region
316 around the focal SNP (see Methods for details). It is predicted that NILs homozygous
317 for the Shahdara (Sha) allele exhibit a more selfish and competitive, and lines
318 homozygous for the Bayreuth (Bay) allele a more cooperative strategy. To separate
319 effects of Sha and Bay alleles from the general genetic background of the respective
320 NILs, we replicated this design with four different pairs of NILs, i.e. in four different
321 genetic backgrounds. In accordance with classic social dilemmas in evolutionary
322 game theory (e.g. prisoner's dilemma) [36], we assumed the competitive genotypes
323 would receive the highest payoff when growing with a cooperative neighbor (**Fig.**
324 **6A)**. However, such payoffs are difficult to quantify directly, and therefore we refer
325 to payoffs as the reduction in above-ground biomass of plants competing relative to
326 plants grown individually (e.g. small reduction in competition = high payoff, etc.).
327 We thus ran replicated experiments matching focal plants with neighbors so that all
328 four possible combinations of Sha and Bay alleles were realized. All genotypes were
329 also grown individually without neighbor, and the relative reduction of individual
330 performance in competition was used to quantify the cost of growing with a specific
331 neighbour.

332 Unexpectedly, the experiment was invaded by a parasite which affected genotypes
333 and allele carriers differentially and influenced competitive outcomes. Over the
334 course of the experiment, some plants showed early leaf blotching and at harvest
335 many showed senesced and wilted leaves (**Fig. 6B** and Supplementary **Fig. S5**). This
336 is a phenotype typical of soil-borne diseases. The symptoms were dependent on
337 genotype, and were mainly seen in NIL-background 33RV113 and individuals
338 carrying the competitor (Sha)-allele, (**Fig. 6C**). At the same time, we detected
339 abundant spores of the obligate plant parasite *Olpidium brassicaea* in roots of all

340 sampled pots (n = 18; Supplementary **Fig. S5**). We took advantage of this to test the
341 hypothesis that the allele increasing cooperation also conferred pathogen resistance.
342 As a proxy for root disease expression, we visually scored root yellowing/browning,
343 a phenotype caused by *O. brassicae* [37]. We found that this score significantly
344 depended on genetic background (ordinal logistic regression p-value < 0.001 for NIL
345 pair) and was always lower in genotypes carrying the cooperative (Bay) allele
346 (ordinal logistic regression p-value = 0.001; **Fig. 6C**).
347 As predicted, plants carrying the allele promoting cooperation were competitively
348 inferior when matched with a competitive neighbor, but only in the two genetic
349 backgrounds that showed low disease expression (**Fig. 6D**). In the two genetic
350 backgrounds with high disease expression, the competitive relationship was very
351 different; most pronounced in the most susceptible genetic background, the genotype
352 carrying the allele promoting cooperation was competitively superior.
353 Together, our results suggest that the cooperative allele is associated with
354 increased resistance against several diseases, which may confer a competitive
355 advantage under high disease pressure. This effect may be caused by antagonistic
356 pleiotropy or by different alleles at closely-linked genes. Whether or not such a
357 trade-off between competition and disease resistance affects selection in nature will
358 have to be tested. However, it could explain why a cooperative allele is maintained in
359 a natural population and over such a wide geographic range.
360

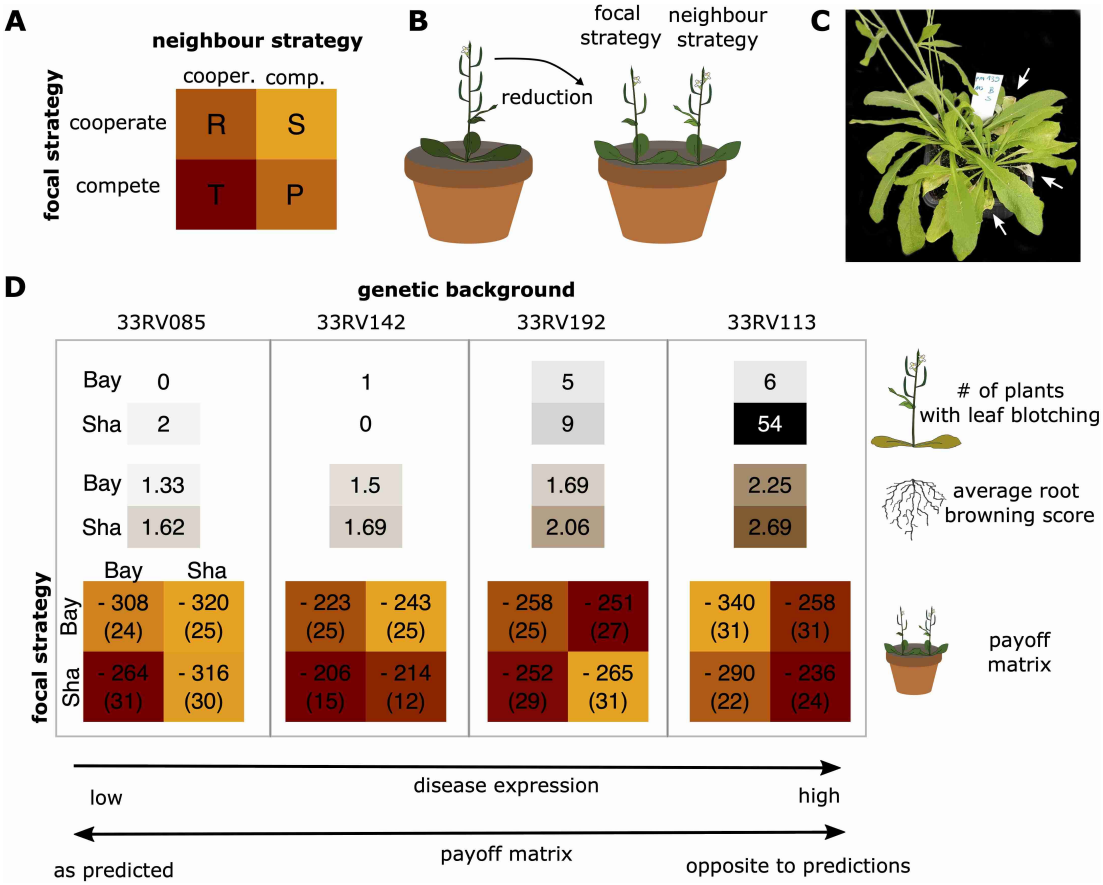


Figure 6: A trade-off between competitive dominance and disease resistance expressed in different near-isogenic lines (A) Expected payoff matrix of interactions between plants ("cooperate" vs. "compete", as determined by carrying Bay vs Sha alleles), with Temptation (T) > Reward (R) > Punishment (P) > Sucker's Payoff (S) (color coded). **(B)** Experimental outline: benefits refer to the cost reduction as measured by the average above-ground biomass of genotypes in competition compared to the biomass of the plant grown alone. A strong reduction refers to a high costs and therefore low benefit, a weak reduction to a high benefit. **(C)** Pot containing a pair of near-isogenic plants isolated from the RIL parent 33RV113. The plant carrying the competitive Sha allele exhibits strong signs of leaf wilting (arrows). **(D)** Summary of the competition experiment, separated by genetic background (33RV085, 33RV142, 33RV192, 33RV192), showing disease symptoms (number of plants exhibiting leaf blotching; root browning score) and payoff matrices for all genetic backgrounds and allele combinations. The values in payoff matrix are the average biomass reduction ± standard error of the mean in brackets

Discussion

Here we used specifically-designed competition experiments, combined with genetic association mapping, to identify (1) plant genotypes that perform well when grown in high-density stands, and (2) potential genes and alleles that underlie these cooperative growth strategies. Interestingly, in *A.thalina* we detected a specific allele that is associated with increased growth in high-density stands, representing a strategy we here refer to as "cooperation". The importance of cooperation among individuals for agronomic production has long been recognized. Animal breeding has focused more explicitly on cooperation and social strategies [19,38]. Domesticated animals are often kept at relatively high densities, which can trigger aggressive behavior among individuals, resulting in high levels of stress, injuries, and increased mortality, all of which are detrimental to animal welfare and productivity. A breeding objective thus has been to obtain relatively docile, cooperative animals that limit adverse interactions when kept at high densities [39]. Conceptually similar considerations apply to plant communities. However, in plants, the traits that underlie cooperation are less easily recognized. In general, such traits may be related to resource sharing in the sense that resources remain accessible to the individuals that most efficiently convert these into biomass or yield. In other words, any excessive investment into competition in the presence of neighbors undermines what is, from an agronomic perspective, an efficient use of resources at the group-level [40–46]. In plants, cooperative growth strategies thus may be characterized by a relative insensitivity to the presence of neighbors, or even a reduction in the development of competitive structures. Indeed, improved group functioning was observed in crop experiments where genotypes exhibited more vertical leaf angles [47], where leaf area [48] or branch numbers were reduced [49], or where belowground competition was experimentally prevented [41,46]. Common to all these experiments is the finding that restricting competitive interference between neighbours, either experimentally or by using genotypes with corresponding traits, is beneficial for group yield, especially at high planting densities. In our study, we observed a lower relative investment into root growth in cooperative genotypes, which is in line with this consideration.

Cooperation, though beneficial for group yield, is typically also associated with individual fitness costs in non-cooperative environments, i.e. under strong competition. Addressing this group-vs.-individual (G-I) trade-offs thus is key to identifying and using cooperative genotypes. In breeding, different strategies have been developed that achieve this goal. First, cooperation can be selected for by anticipating corresponding ideotypes possessing traits expected to foster cooperative strategies. This has been very successfully accomplished during the Green Revolution [6,12,13,50], and lead to the recognition of the relevance of a G-I trade-off in crop improvement [14,17]. Second, cooperative strategies can be directly selected for at the group level [51,52]. For example, this is often done in field trials with maize in which identical hybrid genotypes are planted and evaluated in high-density rows and subsequently in larger field plots. Such a selection at the group level also promotes traits that benefit group yield, for example reduced tassel size, more vertical leaves, and reduced tillering [23,52,53]. Finally, genomic predictions are increasingly adopted to predict a genotype's merit purely based on its genome, whereby prediction models are trained on yield variation of high-density stands of pure varieties. These approaches have arguably contributed to historical and contemporary yield advances, and implicitly or explicitly include elements that selected to some extent for cooperative traits [51]. The method we present here – while motivated by the same broader topic – differs in important respects. First, it directly assesses the group-vs-individual trade-off rather than group yield. By exposing genotypes to two 'social environments' that represent different ends of the cooperation-competition continuum, genotypes expressing cooperative traits can more easily be distinguished. This contrasts with other methods that either focus only on groups (e.g. row or plot-level selection) or use an environment with mixed neighborhoods (e.g. typical setting in quantitative genetic analyses of indirect genetic effects [19,54,55]). Second, our method systematically decomposes group yield into two effects: general vigour and cooperation. This separation is critical because alleles promoting cooperation may be found at low frequency and in genotypes with low vigour. A prominent example is the recessive rice semi-dwarf allele *sd1*. It was originally found in the Taiwanese "Dee-Geo-Woo-Gen" variety, which showed only average yields in the tropics, but was instrumental for boosting tropical rice yields

[9,10,17]. Third, the fact that we use an empirical, heuristic relationship to correct for general vigour implicitly accounts for non-linear relationships between genetics and productivity, which is typically difficult to address with other methods.

In combination with genetic mapping, our method provides an "agnostic" approach to discover latent genetic variation for cooperation. In our proof-of-concept study, we identified a genetic variant of large effect. This was surprising, since traits underlying individual growth and yield or environmental adaptations such as drought tolerance are often highly polygenic [56–58]. On the other hand, there is now increasing evidence that different plant-plant interactions can be affected by few genetic variants of large effects [59,60, this study], maybe resembling the pattern more generally found in plant-parasite-interactions [61]. Regardless of the reason, the existence of such alleles is important given that many biotechnological methods, including genome editing, typically rely on the availability of traits that are influenced by a single or few genes. We therefore propose that biotechnological and breeding research should extend its focus beyond the performance of individuals, often grown as single plants in pots on "conveyor-belt systems", towards the performance of groups and the relevant competitive interactions that drive it.

In this work, we focused – primarily for the sake of simplicity – on a model population of *Arabidopsis thaliana*. This is a first case study using the proposed methodology, and a larger-scale systematic search may reveal alleles with comparable effects in crops or their wild relatives. Here, we found that the allele for cooperation among plants remained relatively frequent (18%) in natural populations, likely because it conferred resistance to diseases to the individuals carrying this allele, and thereby higher fitness under high disease pressure. This raises hopes that crops and wild plants may also hold hidden cooperative traits that have persisted despite their disadvantages in competitive situations. Once identified, such latent variation in cooperation could rapidly be co-opted in marker-assisted breeding programs or through biotechnology. At a more fundamental level, the finding that large-effect genetic variants for cooperation are maintained in natural populations leads to the intriguing thought that social traits could arise as evolutionary exaptations, i.e. by co-option of an existing trait unrelated to cooperation [62].

472 ## Materials and Methods

473 Plant material

474 The natural *A. thaliana* accessions used (Supplementary Dataset S1) are a subset
475 of the RegMap population [25] for which a comprehensive list of traits has been
476 collected [30]. For pairs of near-isogenic lines isolated from four Bay-Sha RILs, we
477 confirmed homozygosity for a genetic polymorphism upstream of the focal SNP
478 (primer F: 5'-TGAGAGAGAGCTGATGATGGATG-3'; primer R: 5'-
479 CGCCTTGATTGACACAGATTC-3'; approx. 100 bp deletion in Sha sequence at position
480 15'333'951) and a genetic polymorphism downstream of the focal SNP by the use of
481 PCR markers (markers primer F: 5'-GCAAGAGGGAGCTAAAGAAACAG-3'; primer R:
482 5'-GCCCTTATCGCCATGAACTG-3'; approx. 50 bp deletion in Sha sequence at position
483 14'914'025). These deletions in the Sha sequence were predicted by the Polymorph
484 tool (http://polymorph.weigelworld.org). All eight genomes were also re-sequenced
485 on the DNBseq plattform (BGI, Hongkong) with a minimum of three Gb sequences
486 per genome. The reads were aligned to the *Arabidopsis* Col-0 reference sequence
487 with the use of the bwa software (version 0.7.16a) [63], and read sorting and variant
488 calling was performed using samtools (version 1.5) [64]. Whole-genome
489 reconstruction was performed as described previously [59], following the approach
490 developed by Xie and colleagues. Genome reconstructions were in agreement with
491 the published marker maps of the corresponding RILs ([35] **Supplementary Fig.**
492 **S5A**). We confirmed genetic differentiation of each of the four NIL-pairs at the locus
493 of interest. Two pairs were otherwise completely isogenic, the two other pairs
494 showed some residual genetic differences on other chromosomes (**Supplementary**
495 **Fig. S5B**).
496

497 Experimental Design

498 Competition experiment: pairs of individual plants were grown in small pots in a
499 factorial design in which the 97 genotypes of the panel were each grown together
500 with one of ten tester genotypes (Bay-0, C24, Col-0, Cvi-0, Ler-1, Sav-0, Sf-2,
501 Shahdara, St-0, Uk-1). The tester genotypes were a subset of the panel, but tester
502 genotypes not part of the original panel would have worked equally well. Each

genotype was further grown in a monoculture of two individuals. Each genotype composition was replicated twice, in separate blocks. In the second block, not enough seeds were available for line LP-2-6; in the second block, we therefore replaced this accession by Kn-0. We thus effectively had 98 genotypes grown with the ten tester accessions. Overall, the experiment consisted of 2134 pots with two plants each. Each tester line was also grown as individual plant, once per block. Pots containing single plants, and pots in which one plant died at the seedling stage, were excluded from data analyses.

Density gradient: to test for decreased self-inhibition in plants carrying the cooperation-associated allel, a plant density gradient was constructed. Six genotypes that carried the cooperation-associated allele (Bor-4, Est-1, Mt-0, Ra-0, Sav-0, Wa-1) but varied in average individual performances were paired with seven genotypes (An-1, Br-0, Can-0, Kondara, Nfa-10, Shahdara, St-0) that carried the alternative allele but had similar average individual performances. By matching genotypes by size, we were able to separate the size-dependence of self-inhibition from the allele effect.

Preparation of plant material and growth conditions

Competition experiment: seeds of all accessions were sown directly onto soil (four parts Einheitserde ED73, Gebrüder Patzer, Germany; one part quartz sand) in February 2016. For germination, the pots of size 6×6×5.5 cm from a given block were randomly placed into trays covered with plastic lids. The two plants per pot were established 3–4 cm apart by sowing 5-20 seeds per position and, once seeds had germinated, removing surplus seedlings. Block 1 and 2 were sown on February 17th and 18th, 2016, respectively. Plants were grown with a photoperiod of 14 hours, providing additional light when necessary. Day-time and night-time temperatures were maintained around 20–25°C and 16–20°C, respectively. Trays were randomly re-arranged within the greenhouse every 3-5 days. After 5-5.5 weeks, pots were transferred from trays onto three tables with automated watering and randomly re-arranged every week. Flowering shoots of individual plants were tied to wooden sticks when they grew taller than approx. 10 cm. All plants were harvested on April 14th (Block 1) and April 15th (Block 2), 2016, i.e. approx. eight weeks after sowing.

535 Each plant was cut below the rosette and individually dried at 65°C for 4-5 days and
536 then stored at room temperature until weighing. Roots from a pot were washed on a
537 metal sieve, and total root mass determined after drying at 65°C for four days.
538 Flowering time was determined by checking every 2–3 days whether flowering bolts
539 were present that exceeded 0.5 cm height.

540 Density gradient: monocultures were sown in pots of 9×9×10 cm (inner pot
541 diameter ~ 8×8 cm) at densities of either 9, 16 or 25 plants per pot. Soil and growth
542 conditions were as described above for the competition experiment. Because we
543 observed some seedling mortality early in the experiment, realized planting density
544 was determined from photographs taken 27 days after sowing, i.e. at a time when
545 competition still was very limited. 54 days after sowing, above-ground biomass was
546 harvested, dried, and weighed.

547 Independent biomass allocation measurements: For an independent assessment of
548 root-to-shoot biomass ratios in the studied natural accessions, 80 genotypes that were
549 used in the main competition experiment were grown for 43 days either as single
550 plants or as monoculture (consisting of four plants per pot) and in pots of 7×7×8 cm
551 size on a mixture of one part ED73 and four parts quartz sand. The measurements
552 were performed as described above.

553 Competition experiments with NIL-pairs: we used four NIL-pairs derived from
554 33RV085, 33RV113, 33RV142 and 33RV192. Each pair consisted of one line
555 carrying the Bay allele and one line carrying the Sha allele. For each pair, we grew
556 16 monocultures per line and 32 mixtures of the two lines, all consisting of two
557 plants per pot. We additionally grew each line as single plants per pot, also replicated
558 16 times. Seeds were directly sown into 6×6×5.5 cm pots filled with a 4:1 parts ED73
559 soil : quartz sand. Leaf blotching and excessive senescence were noticed mid-way
560 through the experiment and scored 31 and 50 days after sowing. Scoring was done
561 blindly, i.e. with no information about pot or genotype identity. Shoot and root
562 biomass were harvested 57 days after sowing, roots washed, and all biomass dried
563 and weighed as described above. Root browning scores were determined visually by
564 categorizing root browing into three ordinary levels (Supplementary **Fig. S6**). Roots
565 were stained using a 1% cotton blue in 80% lactic acid solution and examined using
566 a Leica microscope for a visual inspection of potential root pathogens.

Statistical analyses

All statistical analyses were performed using the statistical software R version 3.4.1 (http://r-project.org). The block-adjusted individual performance of genotypes across mixtures were estimated using least square means from a model including just block and genotype. Monoculture biomass per individual (i.e. total average monoculture biomass divided by two) was then fitted as function of linear and quadratic forms of individual biomass, using the R-function "lm". The G-I trade-off value was determined as orthogonal distance by determining the point in the quadratic heuristic that was closest to the respective point by non-linear minimization using the R-function "nlm". The GWAS analyses were performed with easyGWAS (https://easygwas.ethz.ch) [65], using the EMMAX algorithm [66] and using SNPs from the 250k SNP chip (http://bergelson.uchicago.edu/) or the 1001 genomes project (http://1001genomes.org/) [27]. SNPs with a minor allele frequency below 5% were removed.

For the density gradient experiment, productivity was modelled in dependence of the fixed terms area per individual, allele, plus their interaction. The corresponding random terms were accession, and the interaction between accession and area per individual. Individual performance in mixture of the previous experiment was included as a covariate in the model, because it was used in the design of the experiment for stratified sampling of genotypes according to size. The realized densities deviated from sown densities because of a relatively high initial mortality. Therefore, we instead used densities determined from photographs of each pot that were made mid-way through the experiment. Two pots were removed from the analysis because realized densities were much higher than planted densities, probably because they accidentally had not been thinned to the intended densities. In the NIL-pair competition experiment, the payoff for a given combination of strategies was determined as shoot mass of a line grown as individual plant minus its shoot mass under competition, i.e. the payoff quantified the shot biomass reduction induced by to the presence of particular neighbours. The standard error of the payoff σ_{payoff} was calculated by error propagation as $\sqrt{(\sigma^2_{single\ plant} + \sigma^2_{individual\ |\ neighbour})}$.

Root browning scores were analyzed using an ordinal logit regression as implemented in the polr-function of the R package MASS, with ordinal root scores as independent variable and community type (single plant or monoculture), genetic background (NIL pair) and allele (Sha or Bay) as explanatory variables. Mixtures were excluded from the analysis of root browning scores.

Acknowledgements

We thank Bernhard Schmid (UZH) and Andrea Patocchi (Agroscope) for support and helpful discussions, Matthias Lutz (Agroscope) for help identifying *Olpidium brassicae* in root samples, Cyrille Violle (CEFE) for helpful comments on the manuscript, Matthias Philipp, Daniel Trujillo and Mariela Soto Araya for help with sowing and harvesting the competition experiment, and Matthias Furler for technical support in the greenhouse. This work was supported by the University of Zurich, Agroscope, an Advanced Grant of the European Research Council (to UG), and an Ambizione Fellowship (PZ00P3_148223) of the Swiss National Science Foundation (to SEW). FV acknowledges funding from the French Agency for Research (ANR grant ANR-17-CE02-0018-01, 'AraBreed'), and the Agreenskills fellowship programme (grant agreement n° 3215), which has received funding from the EU's Seventh Framework Programme under the agreement N° FP7-609398.

Author contributions

SEW, NDP and PAN designed the research, SEW performed the experiments with help from NDP and SL. SEW and PAN performed the analyses and wrote the manuscript with input from JM, FV, and UG. NDP, JM, FV, and UG also contributed technical resources and data. All authors revised and approved the final version of the manuscript.

Data availability

The datasets described and a basic analysis script are available through the Zenodo data repository (DOI:10.5281/zenodo.2659735). More extensive analysis scripts are available from the authors upon request.

Competing interests

The authors declare no competing financial interests.

References

1. Watson A, Ghosh S, Williams MJ, Cuddy WS, Simmonds J, Rey MD, et al. Speed breeding is a powerful tool to accelerate crop research and breeding. Nat Plants. 2018;4: 23–29.
2. Crossa J, Pérez-Rodríguez P, Cuevas J, Montesinos-López O, Jarquín D, de los Campos G, et al. Genomic Selection in Plant Breeding: Methods, Models, and Perspectives. Trends Plant Sci. 2017;22: 961–975.
3. Furbank RT, Tester M. Phenomics - technologies to relieve the phenotyping bottleneck. Trends Plant Sci. 2011;16: 635–644.
4. Ray DK, Ramankutty N, Mueller ND, West PC, Foley JA. Recent patterns of crop yield growth and stagnation. Nat Commun. 2012;3.
5. Ray DK, Mueller ND, West PC, Foley JA. Yield Trends Are Insufficient to Double Global Crop Production by 2050. PLoS One. 2013;8: e66428.
6. Borlaug NE. Wheat Breeding and its Impact on World Food Supply. Third International Wheat Genetics Symposium. 1968. pp. 1–36.
7. Khush GS. Green revolution: the way forward. Nat Rev Genet. 2001;2: 815–821.
8. De Datta SK, Tauro AC, Balaoing SN. Effect of Plant Type and Nitrogen Level on the Growth Characteristics and Grain Yield of Indica Rice in the Tropics1. Agron J. 1968;60: 643–647.
9. Hedden P. The genes of the Green Revolution. Trends Genet. 2003;19: 5–9.
10. Spielmeyer W, Ellis MH, Chandler PM. Semidwarf (sd-1), “green revolution” rice, contains a defective gibberellin 20-oxidase gene. Proc Natl Acad Sci. 2002;99: 9043–9048.

11. Donald CM. Competitive plants, communal plants, and yield in wheat crops. In: Evans LT, Peacock WJ, editors. Wheat Science - Today and Tomorrow. Cambridge University Press; 1981. pp. 223–247.

12. Donald CM. The breeding of crop ideotypes. Euphytica. 1968;17: 385–403.

13. Jennings PR. Plant Type as a Rice Breeding Objective. Crop Sci. 1964;4: 13–15.

14. Jennings PR, De Jesus JJ. Studies on competition in rice I. Competition in mixtures of varieties. Evolution. 1968;22: 119–124.

15. Duvick DN, Smith JSC, Cooper M. Long-Term Selection in a Commercial Hybrid Maize Breeding Program. In: Janick J, editor. Plant Breeding Reviews Part 2 Long Term Selection: Crops, Animals and Bacteria, Vol 24. New York: JohnWiley & Sons; 2004. pp. 109–151.

16. Tsunoda S. A Developmental Aanlysis of Yielding Ability in Varieties of Field Crops: II. The assimilation-system of plants as affected by the form, direction and arrangement of single leaves. Japanese J Breed. 1959;9: 237–244.

17. Jennings PR, Herrera RM. Studies on competition in rice II: Competition in segregating populations. Evolution. 1968;22: 332–336.

18. Peng S, Khush GS, Virk P, Tang Q, Zou Y. Progress in ideotype breeding to increase rice yield potential. F Crop Res. 2008;108: 32–38.

19. Wade MJ, Bijma P, Ellen ED, Muir W. Group selection and social evolution in domesticated animals. Evol Appl. 2010;3: 453–465.

20. Goodnight C. The influence of environmental variation on group and individual selection in a cress. Evolution. 1985;39: 545–558.

21. Murphy GP, Swanton CJ, Van Acker RC, Dudley SA. Kin recognition, multilevel selection and altruism in crop sustainability. J Ecol. 2017;105: 930–934.

22. Dudley SA. Plant cooperation. AoB Plants. 2015;7: plv113.

23. Denison RF. Darwinian Agriculture. Princeton, NJ: Princeton Univ. Press; 2012.

24. Weiner J, Du YL, Zhang C, Qin XL, Li FM. Evolutionary agroecology: individual fitness and population yield in wheat (Triticum aestivum). Ecology. 2017;98: 2261–2266.

25. Horton MW, Hancock AM, Huang YS, Toomajian C, Atwell S, Auton A, et al. Genome-wide patterns of genetic variation in worldwide Arabidopsis thaliana accessions from the RegMap panel. Nat Genet. 2012;44: 212–216.

26. Laird RA, Aarssen LW. Size inequality and the tragedy of the commons phenomenon in plant competition. Plant Ecol. 2005;179: 127–131.

27. Alonso-Blanco C, Andrade J, Becker C, Bemm F, Bergelson J, Borgwardt KM, et al. 1,135 genomes reveal the global pattern of polymorphism in Arabidopsis thaliana. Cell. 2016;166: 481–491.

28. York LM, Galindo-Castañeda T, Schussler JR, Lynch JP. Evolution of US maize (Zea mays L.) root architectural and anatomical phenes over the past 100 years corresponds to increased tolerance of nitrogen stress. J Exp Bot. 2015;66: 2347–2358.

29. Zhu YH, Weiner J, Yu MX, Li FM. Evolutionary agroecology: Trends in root architecture during wheat breeding. Evol Appl. 2018;00: 1–11.

30. Atwell S, Huang YS, Vilhjálmsson BJ, Willems G, Horton M, Li Y, et al. Genome-wide association study of 107 phenotypes in Arabidopsis thaliana inbred lines. Nature. 2010;465: 627–631.

31. Nowak MA. Five rules for the evolution of cooperation. Science. 2006;314: 1560–1563.

32. Todesco M, Balasubramanian S, Hu TT, Traw MB, Horton M, Epple P, et al. Natural allelic variation underlying a major fitness trade-off in Arabidopsis thaliana. Nature. 2010;465: 632–636.

33. Nomura K, DebRoy S, Lee YH, Pumplin N, Jones J, He SY. A bacterial virulence protein suppresses host innate immunity to cause plant disease. Science. 2006;313: 220–223.

34. Nemri A, Atwell S, Tarone AM, Huang YS, Zhao K, Studholme DJ, et al. Genome-wide survey of Arabidopsis natural variation in downy mildew resistance using combined association and linkage mapping. Proc Natl Acad Sci. 2010;107: 10302–10307.

35. Loudet O, Chaillou S, Camilleri C, Bouchez D, Daniel-Vedele F. Bay-0 x Shahdara recombinant inbred line population: A powerful tool for the genetic dissection of complex traits in Arabidopsis. Theor Appl Genet. 2002;104: 1173–1184.

36. Axelrod R, Hamilton WD. The evolution of cooperation. Science. 1981. pp. 1390–1396.

723 37. Van Der Meer JHH. The rhizoctonia- and olpidium disease of cauliflower
724 seedlings. Tijdschr Over Plantenziekten. 1926;32: 235–242.

725 38. Muir WM. Group selection for adaptation to multiple-hen cages: Selection
726 program and direct responses. Poult Sci. 1996;75: 447–458.

727 39. Friedrich J, Brand B, Schwerin M. Genetics of cattle temperament and its
728 impact on livestock production and breeding – a review. Arch Anim Breed.
729 2015;58: 13–21.

730 40. Falster DS, Westoby M. Plant height and evolutionary games. Trends Ecol
731 Evol. 2003;18: 337–343.

732 41. Gersani M, Brown JS, O'Brien EE, Maina GM, Abramsky Z. Tragedy of the
733 commons as a result of root competition. J Ecol. 2001;89: 660–669.

734 42. Cabal C, Martínez-García R, De Castro Aguilar A, Valladares F, Pacala SW.
735 The exploitative segregation of plant roots. Science. 2020;370: 1197–1199.

736 43. Anten NPR, Vermeulen PJ. Tragedies and Crops: Understanding Natural
737 Selection To Improve Cropping Systems. Trends Ecol Evol. 2016;31: 429–439.

738 44. Zhang DY, Sun GJ, Jiang XH. Donald's ideotype and growth redundancy: A
739 game theoretical analysis. F Crop Res. 1999;61: 179–187.

740 45. Zhu L, Zhang DY. Donald's Ideotype and Growth Redundancy: A Pot
741 Experimental Test Using an Old and a Modern Spring Wheat Cultivar. PLoS
742 One. 2013;8: e70006.

743 46. Zhu Y-H, Weiner J, Li F-M. Root proliferation in response to neighbouring
744 roots in wheat (Triticum aestivum). Basic Appl Ecol. 2019;39: 10–14.

745 47. Tian J, Wang C, Xia J, Wu L, Xu G, Wu W, et al. Teosinte ligule allele
746 narrows plant architecture and enhances high-density maize yields. Science.
747 2019;365: 658–664.

748 48. Srinivasan V, Kumar P, Long SP. Decreasing, not increasing, leaf area will
749 raise crop yields under global atmospheric change. Glob Chang Biol. 2017;23:
750 1626–163.

751 49. Kokubun M. Design and examination of soybean ideotypes. Japan Agric Res
752 Q. 1987;21: 237–243.

753 50. Vogel OA, Craddock JC, Muir CE, Everson EH, Rohde CR. Semidwarf
754 Growth Habit in Winter Wheat Improvement for the Pacific Northwest1.
755 Agron J. 1956;48: 76–78.

51. Murphy GP, Swanton CJ, Van Acker RC, Dudley SA. Kin recognition, multilevel selection and altruism in crop sustainability. J Ecol. 2017;105: 930–934.

52. Weiner J. Looking in the Wrong Direction for Higher-Yielding Crop Genotypes. Trends Plant Sci. 2019;19: S1360-1385.

53. Denison RF. Evolutionary tradeoffs as opportunities to improve yield potential. F Crop Res. 2015;182: 3–8.

54. Costa E Silva J, Potts BM, Gilmour AR, Kerr RJ. Genetic-based interactions among tree neighbors: Identification of the most influential neighbors, and estimation of correlations among direct and indirect genetic effects for leaf disease and growth in Eucalyptus globulus. Heredity. 2017;119: 125–135.

55. Camerlink I, Ursinus WW, Bijma P, Kemp B, Bolhuis JE. Indirect Genetic Effects for Growth Rate in Domestic Pigs Alter Aggressive and Manipulative Biting Behaviour. Behav Genet. 2015;45: 117–126.

56. Lynch M, Walsh B. Genetics and Analysis of Quantitative Traits. Sinauer, Sunderland, Mass. 1998.

57. Boyle EA, Li YI, Pritchard JK. An Expanded View of Complex Traits: From Polygenic to Omnigenic. Cell. 2017; 169: 1177–1186.

58. Wieters B, Steige KA, He F, Koch EM, Ramos-Onsins SE, Gu H, et al. Polygenic adaptation of rosette growth in Arabidopsis thaliana. PLoS Genet. 2021;17: e1008748.

59. Wuest SE, Niklaus PA. A plant biodiversity effect resolved to a single chromosomal region. Nat Ecol Evol. 2018;2: 1933–1939.

60. Montazeaud G, Flutre T, Ballini E, Morel J-B, David J, Girodolle J, et al. From cultivar mixtures to allelic mixtures: opposite effects of allelic richness between genotypes and genotype richness in wheat. New Phytol. 2022;233: 2573–2584.

61. Wilfert L, Schmid-Hempel P. The genetic architecture of susceptibility to parasites. BMC Evol Biol. 2008;8: 187.

62. Gould SJ, Vrba ES. Exaptation—a Missing Term in the Science of Form. Paleobiology. 1982;8: 4–15.

63. Li H, Durbin R. Fast and accurate short read alignment with Burrows – Wheeler transform. Bioinformatics. 2009;25: 1754–1760.

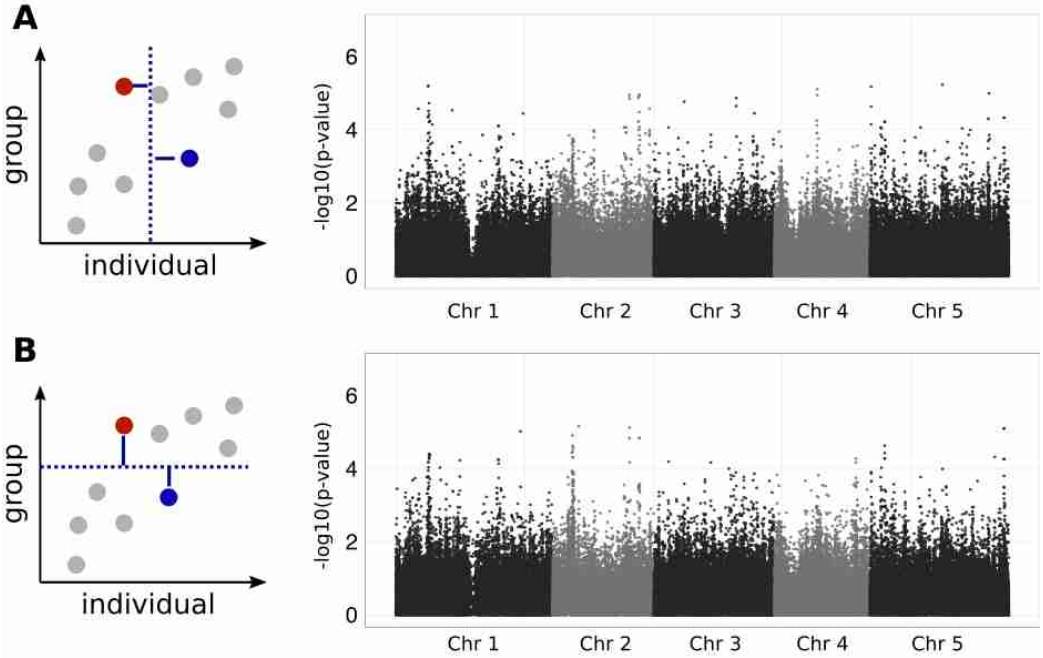
789 64. Li H, Handsaker B, Wysoker A, Fennell T, Ruan J, Homer N, et al. The
790 Sequence Alignment/Map format and SAMtools. Bioinformatics. 2009;25:
791 2078–2079.

792 65. Grimm DG, Roqueiro D, Salomé PA, Kleeberger S, Greshake B, Zhu W, et al.
793 easyGWAS: A Cloud-Based Platform for Comparing the Results of Genome-
794 Wide Association Studies. Plant Cell. 2016;29: 5–19.

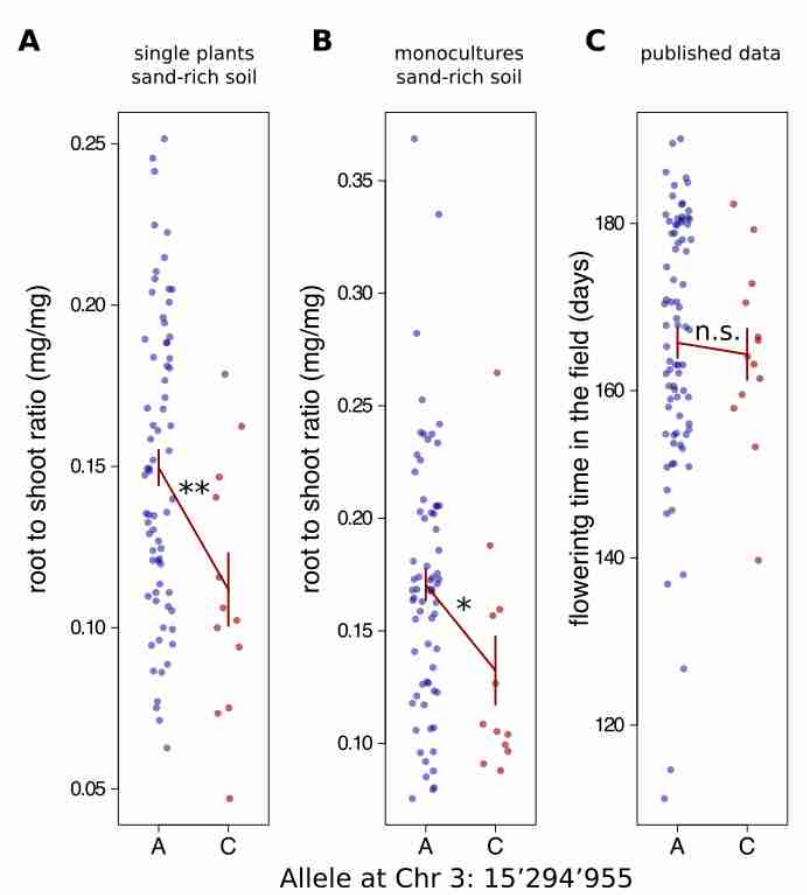
795 66. Kang HM, Sul JH, Service SK, Zaitlen NA, Kong SY, Freimer NB, et al.
796 Variance component model to account for sample structure in genome-wide
797 association studies. Nat Genet. 2010;42: 348–354.

Supplemental Material

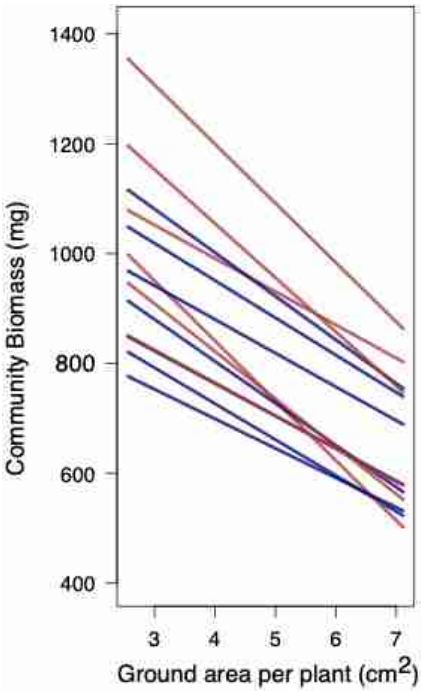
Supplementary Figure S1: Experimental setup of the competition experiment. (A)-(C) Photos show the experiment at sowing (**A**), midway through the experiment (**B**) and at harvest day (**C**).



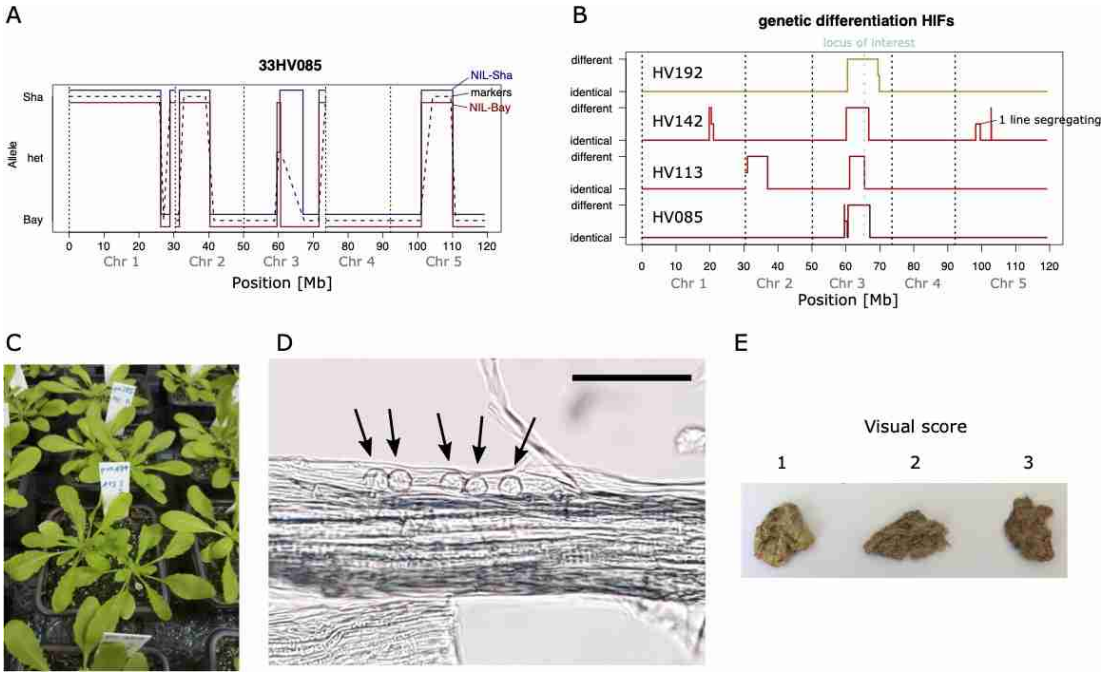
Supplementary Figure S2. Association tests for variation in (A) average individual performance across mixtures or (B) average monoculture performance.



Supplementary Figure S3. Associations of SNP Chr3:15'294'955 with phenotypic variation in traits related to plant strategies. (A) and **(B)** Shoot-to-root ratios for genotypes grown in monocultures (A) or as individual plants (B) in an independent experiment and on sand-rich soil are shown. **(C)** Published data of genotypic means in flowering time in the field [30] . Bars show mean ± s.e. ** = ANOVA $p < 0.01$; * = ANOVA $p < 0.05$; n.s. not significant.



Supplementary Figure S4: Decreased self-inhibitiion of genotypes carrying the cooperation-associated allele along a density gradient Lines represent reaction norms or genotypes carrying different alleles at Chr 3 SNP 15'294'955; red lines: cooperator allele carriers; blue lines: competitor allele carriers



Supplementary Figure S5: A trade-off between competitive dominance and disease resistance. (A) Genome reconstructions of two near-isogenic lines (NILs) from the 33RV085 parental RIL. Viterbi paths of each NIL are shown in red (Bay-allele at Chr3:15'294'955) and blue (Sha-allele), together with published marker data of the parent (dashed line). **(B)** Genetic differences identified in whole-genome comparisons between the pairs of near-isogenic lines. All NIL-pairs differ from each other at Chr3:15'294'955 (light blue: "locus of interest"). **(C)** Earliest sign of shoot-level disease expression in line 33RV113 carrying the Sha-allele. **(D)** Microscopic image of dried root samples containing resting spores of the obligate parasite *Olpidium brassicae* (arrows). Scale bar = 50 μm. **(E)** Visual scoring scheme of root browning for washed and dried root samples from the competition experiment. Scoring was performed fully blinded to the sample ID or genotype.

Supplementary Dataset S1: List of *A. thaliana* accessions used in the study, their estimated productivities across mixtures and monocultures, and measured trait values.